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RED-TAILED HAWK NEST SITES IN PUERTO RICO

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ABSTRACT.—We describe Red-tailed Hawk (*Buteo jamaicensis*) nest sites in four habitats in Puerto Rico. Forty-nine nests were located in 21 species of trees. Red-tailed Hawks nested in trees that were taller than the mean canopy height of trees in surrounding plots and that allowed a view of at least 50% of their territory. Most nests were in the upper third of the tree on horizontal branches and secondary crotches. Vines and epiphytes commonly supported nests. Differences in nest-site parameters among different habitat types reflected major dissimilarities in vegetation, topography, climate, and land-use patterns. Nest plots in the dry lowlands were farther from water, had fewer species of trees, and shorter nest trees than nest plots in the other habitat types. Because they occurred mostly in grazed or recently abandoned pastures, nest plots in the dry lowlands also had less-developed shrub layers and greater ground cover. Like their continental North American counterparts, Red-tailed Hawks in Puerto Rico nested in sites that offered a wide view of the territory. *Received 21 Oct. 1985, accepted 2 June 1986.*

RESUMEN.—Describimos los sitios de anidamiento del Guaraguao en cuatro hábitats en Puerto Rico. Cuarenta y nueve nidos fueron encontrados en 21 especies de árboles. Los Guaraguaos anidaron en árboles que eran mas altos que la altura promedio del dosel y esto les permitió tener una visibilidad desde el nido de mas del 50% de su territorio. La mayoría de los nidos se encontraron en el parte superior del árbol sobre ramas horizontales y horquetas secundarias. Comunmente los nidos se encontraron apoyados sobre bejucos y plantas epífitas. Las diferencias observadas entre los sitios de anidamiento en los diferentes hábitats reflejaron las diferencias generales entre las zonas de estudio con respecto a vegetación, topografía, clima y patrones del uso de la tierra. Los sitios de anidamiento en las zonas áridas a baja altitud se encontraron mas lejos del agua, tenían menos especies de árboles y tenían árboles de menor estatura que los sitios de anidamiento en los otros hábitats. Por su localización en pastizales y potreros abandonados los sitios de anidamiento en las zonas áridas tenían un estrato arbustivo menos desarrollado y una mayor cubierta vegetal del suelo que los sitios de anidamiento en los otros hábitats. Al igual que los Guaraguaos en América del Norte los Guaraguaos en Puerto Rico anidaron en sitios que ofrecían una vista amplia del territorio.

The nesting habits of Red-tailed Hawks (*Buteo jamaicensis*) in temperate North America have been well described (e.g., Bent 1937, Hagar 1957, Belyea 1976, Howell et al. 1978, Petersen 1979, Titus and Mosher 1981, Bednarz and Dinsmore 1982), but little is known about their nesting habits in the one-quarter of the latitudinal extent of their range that lies

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within the tropics. Here, we present information on Red-tailed Hawk nest sites in four tropical habitats in Puerto Rico at the southeasternmost limit of the geographic range of the species.

STUDY AREA

Puerto Rico is the smallest (8900 km^2) and easternmost island of the Greater Antilles. Approximately 22% of the island has slopes greater than 45%, and it has mountain peaks of up to 1340 m. By 1912 less than 1% of the virgin forests of Puerto Rico remained, and much of the land was converted to pastures and agriculture (Wadsworth 1949). More recently, agricultural activities have declined, and lands have reverted back to forest. Presently, about 30% of the island is classified as forest (Birdsey and Weaver 1982).

We studied the Puerto Rican Red-tailed Hawk (*B. j. jamaicensis*) or "Guaraguao" in four distinct habitats: dry lowlands, moist lowlands, montane rain forest, and montane cloud forest. The dry-lowland study area (altitude range: 0–200 m above sea level) was in southwestern Puerto Rico within the subtropical dry-forest life-zone (Ewel and Whitmore 1973), and it consists primarily of pastures with scattered trees and shrubby areas. Mean annual rainfall is about 90 cm, and mean monthly temperature varies from approximately 23.9 to 28.4°C.

The moist lowland study areas (0–450 m above sea level) were in central and northeastern Puerto Rico at low- and mid-elevations within the subtropical-moist and wet-forest life-zones (Ewel and Whitmore 1973). This habitat is dominated by pastures, small agricultural plots, and patches of secondary forests interspersed along ravines and ridges. Mean annual rainfall varies from about 100 to 300 cm, and mean monthly temperature varies from approximately 20.5 to 27.0°C.

The montane rain-forest and cloud-forest study areas (450–1050 m above sea level) were located within the rugged 11,200-ha Luquillo Experimental Forest in northeastern Puerto Rico. This forest reserve contains the largest expanses of primary forests remaining on the island. Mean annual rainfall is about 400 cm, and mean monthly temperature varies from approximately 19.2 to 25.0°C. At lower elevations the forest canopy reaches heights of approximately 20 m and is comprised of over 150 species of trees. Canopy height and tree species diversity decrease with increasing altitude, and a stunted cloud forest occurs near the summits of the mountains.

The cloud-forest study area was found within the lower-montane rain-forest life-zone (Ewel and Whitmore 1973). Here, high winds are common, and fog reduces solar radiation by 40% (Howard 1970). Mean annual rainfall is about 400 cm, and mean monthly temperature varies from approximately 16.7 to 21.0°C.

METHODS

Field work was conducted from August 1981 to July 1983. We found nests in the lowlands by visiting nest sites reported to us by local residents and by systematically searching for nests along roads. In the rain and cloud forests we climbed emergent trees, cliffs, and observation towers that offered a view above the canopy, and we visually followed adult Red-tailed Hawks that were carrying prey or twigs to their nests.

We sampled the vegetation on nest plots using the methods described by Titus and Mosher (1981), as modified from James and Shugart (1970). Each nest plot consisted of a 0.04-ha circular plot (11.3 m radius) with the nest tree at its center. Table 1 presents a description of the 22 variables measured within each nest plot. Variables 1–4 describe the nest location and the nest tree, variables 5–7 describe distances between the nest tree and specific habitat

TABLE 1
DESCRIPTION OF THE VARIABLES MEASURED AT RED-TAILED HAWK NEST-SITE PLOTS IN PUERTO RICO

Mnemonic code	Description of variable (units)
1. NEST HT	Height of nest (m).
2. HT NST TREE	Height of nest tree (m).
3. P NST HT	Nest height as % of tree height.
4. DBH	Diameter at breast height of nest tree (cm).
5. DIS H2O	Distance to nearest permanent freshwater body (m).
6. DIS FOR OP	Distance to nearest forest opening (m).
7. DIS HUM	Distance from human activity (e.g., houses, roads well-traveled by pedestrians, areas where humans are active >8 h per day) (m).
8. CAN HT	Average canopy height of the plot (m).
9. NO TREES	Number of overstory trees (those trees with crowns at the canopy level).
10. NO SP TREE	Number of species of overstory trees.
11. SHRUB DEN	Shrub density (James and Shugart 1970).
12. SHRUB IND	Shrub index, measured along the same transect as SHRUB DEN, except all woody stems 1–6 cm diameter and 0.25–1.75 m in height are measured; includes SHRUB DEN plus shrubs that do not intersect outstretched arms.
13. CAN TOT[a]	Percentage total canopy cover.
14. UND TOT[a]	Percentage total understory tree (trees with crowns below the canopy level) cover.
15. GRND TOT[a]	Percentage total ground cover (any green vegetation <1 m tall).
16. UND 14	Number of understory stems in the plot with diameter between 1 and 4 cm.
17. UND 58	Number of understory stems 5–8 cm in diameter.
18. UND GT9	Number of understory stems with diameter >9 cm.
19. DBH LT25	Number of overstory trees in the plot with dbh <25 cm.
20. DBH 2650	Number of overstory trees with dbh between 26 and 50 cm.
21. DBH GT50	Number of overstory trees with dbh >50 cm.
22. BASAL	Basal area in m^2/ha for overstory trees.

[a] Mean values based on 40 ocular tube readings, 10 along each of the 4 transects used in SHRUB DEN (James and Shugart 1970).

features, and variables 8–22 describe the vegetation structure. All distances were measured using a Haga altimeter, tape measure, or range finder. We recorded the location of the nest on the tree (e.g., main crotch, horizontal branch, etc.), the position of the nest tree relative to topographic features (e.g., upper or lower half of hill, ridgetop, hollow, etc.), and the directional exposure of the slope (0° = north). We mapped the boundaries of 33 Red-tailed Hawk territories during the breeding season by observing courtship and territorial displays of adults that we recognized by plumage characteristics and by the nest sites they returned to after interacting with neighboring birds. We estimated the proportion of each territory that could be viewed from each nest by climbing to the nest or to a nearby tree and subjectively classifying each nest as allowing a view of <50% or >50% of the territory.

TABLE 2
FREQUENCY OF VINES AND EPIPHYTES AT RED-TAILED HAWK NESTS IN DIFFERENT HABITATS IN PUERTO RICO

Study area	Number of nests	% nests in contact with vines[a]	% nests supported by vines[b]
Dry lowland	6	33	0
Moist lowland	18	61	28
Cloud and rain forest	10	90	70

[a] Differences among study areas were not statistically significant ($\chi^2 = 5.51$, df = 2, $0.05 < P < 0.10$).
[b] Differences among study areas were statistically significant ($\chi^2 = 8.94$, df = 2, $P < 0.025$).

RESULTS

We found 49 nests and measured vegetation parameters on 6 nest plots in the dry lowlands (altitude range: 5–40 m), 30 in the moist lowlands (5–402 m), 2 in the rain forest (490–650 m), and 2 in the cloud forest (750–870 m). The 15 nests described by Laboy (1982) in moist-lowland habitat are included in our sample. We were unable to measure vegetation parameters for 9 of the 49 nests, but we did obtain other information on their nest-site characteristics, which was used in the analyses.

The 49 nests were in 21 species of trees; 8 were in *Hymenaea courbaril,* 6 were in *Cecropia peltata,* 6 were in *Bucida buceras,* 5 were in *Casuarina equisetifolia,* and 3 were in *Spondias mombin.* Forty-seven percent of these nests were located on horizontal branches, 27% on secondary crotches, 20% on the main crotch, and 6% were braced against the trunk. Eighty percent of 40 nests were in the upper third of the tree. In 76% of 33 plots that contained three or more trees, Red-tailed Hawks selected a tree taller than the average canopy height of the plot ($\chi^2 = 10.94$, df = 1, $P < 0.05$).

Ten species of vines and epiphytes were in contact with 65% of 34 nests and were an important source of support for 29% of the nests (Table 2). Three nests were completely supported by vines or epiphytes and did not touch branches of the nest tree. The incidence of vines and epiphytes at nests increased progressively from dry to wet habitats (Table 2). In the rain and cloud forests 70% of the nests were not visible from the ground due to the screening effect of vines. Vines and epiphytes in contact with nests included *Paullinia pinnata* (Sapindaceae), *Securidaca virgata* (Polygalaceae), *Odontosoria aculeata* (Polypodiaceae), *Macfadyena unguis-cati* (Bignoniaceae), *Philodendron oxycardium* (Araceae), *Symphysia racemosa* (Ericaceae), *Schlegelia brachiantha* (Scrophulariaceae), *Clusia gundlachii* (Clusiaceae), *Marcgravia sintenisii* (Marcgraviaceae), and *Guzmania* sp. (Bromeliaceae).

Fifty-three percent of the nest trees were on the upper half of a hill, 22% on the lower half or in the bottom of a valley, and 25% in flat areas. In 82% of 33 nests an adult at the nest could view >50% of its territory. The hillsides where the nests were located did not face any particular direction ($\chi^2 = 9.04$, df = 7, $P > 0.05$). Thirty-six percent of 35 nests in our dry-lowland and moist-lowland study areas were within 300 m of human activity; one was 29 m away from a house. Only one of 16 nests that were inspected in two consecutive breeding seasons was reused.

Nest plots in the dry lowlands were farther from water, had fewer species of trees, and shorter nest trees than nest plots in the other habitat types (Table 3). Because they occurred mostly in grazed or recently abandoned pastures, nest plots in the dry lowlands also had less-developed shrub layers and greater ground cover. The high values of NEST HT, HT NST TRE, DBH, and CAN HT for the rain-forest plots probably reflected the abundance of tall trees in that habitat. The low number of nest plots in the rain and cloud forest did not allow us to compare them statistically with nest plots in the other habitat types.

DISCUSSION

Techniques developed in temperate North America for nest-site habitat analysis worked fairly well in Puerto Rico, but a few problems were encountered. In some nest plots the crown of the nest tree covered the entire 0.04-ha plot, accounting for 100% canopy cover. Many of the stems we tallied in moist-lowland, rain-forest, and cloud-forest plots were actually woody lianas hanging down from the canopy of the nest tree. Measuring the diameter, angle, and number of branches supporting the nest was often meaningless because of the presence of numerous vines and epiphytes that also offered support to the nest.

Differences in nest-site parameters among the different habitat types (Table 3) reflected major dissimilarities in vegetation, topography, climate, and land-use patterns. Santana and Temple (in press) found that the percent coverage of pastures within Red-tailed Hawk territories was 84%, 47%, 0%, and 0% in the dry-lowland, moist-lowland, rain-forest, and cloud-forest habitats, respectively. Whereas, the percent coverage of shrubland and forest was 10%, 43%, 99%, and 99%, respectively. Nest-site characteristics reflected these general landscape differences. Mosher et al. (1986) and Titus (1984) have shown for other species of raptors that nest-site habitat differences among regions are partly due to differences in the structure of available habitat in each region.

Unlike their temperate-zone counterparts, hawks in the humid tropics commonly use vines and epiphytes as a source of support for their nests (Wiley and Wiley 1981, Delannoy 1984, Griffin 1985). The incidence of

TABLE 3

RED-TAILED HAWK NEST-SITE CHARACTERISTICS IN FOUR DIFFERENT HABITATS IN PUERTO RICO

Variable	Dry lowland	Moist lowland	Rain forest	Cloud forest
NEST HT	9.9 ± 3.7 (6)[a]	14.9 ± 7.0 (30)	21.6 ± 1.5 (2)	13.2 ± 1.4 (2)
HT NST TREE	12.3 ± 3.4 (6)[b]	18.4 ± 6.8 (30)	26.6 ± 1.0 (2)	19.8 ± 1.1 (2)
P NST HT	76.6 ± 14.5 (6)	79.2 ± 14.6 (30)	81.9 ± 9.0 (2)	66.8 ± 10.7 (2)
DBH	66.2 ± 18.7 (6)	73.7 ± 34.3 (30)	94.9 ± 5.8 (2)	51.2 ± 6.6 (2)
DIS H2O	427.3 ± 291.9 (6)[c]	166.3 ± 160.3 (31)	38.0 ± 11.3 (2)	46.5 ± 64.3 (2)
DIS HUM	667.7 ± 475.3 (6)	475.5 ± 433.1 (29)	917.0 ± 1060.7 (2)	1773.5 ± 327.6 (2)
DIS FOR OP	33.3 ± 57.7 (3)	31.9 ± 35.9 (26)	96.0 ± 5.6 (2)	100.0 ± 0.0 (2)
CAN HT	10.2 ± 0.6 (3)[c]	15.8 ± 5.1 (26)	20.2 ± 0.3 (2)	13.2 ± 4.4 (2)
NO TREES	3.3 ± 3.0 (6)	8.1 ± 6.7 (31)	7.5 ± 0.7 (2)	18.0 ± 14.1 (2)
NO SP TREE	1.5 ± 0.8 (6)[c]	3.4 ± 1.7 (31)	5.5 ± 0.7 (2)	5.5 ± 3.5 (2)
SHRUB DEN	9.7 ± 12.9 (6)[c]	47.5 ± 28.8 (30)	23.5 ± 4.9 (2)	26.5 ± 2.1 (2)
SHRUB IND	29.2 ± 35.8 (6)[b]	83.9 ± 48.6 (30)	38.0 ± 0.7 (2)	50.0 ± 2.8 (2)
CAN TOT	57.3 ± 23.5 (6)	74.1 ± 20.2 (30)	99.0 ± 0.7 (2)	94.0 ± 8.5 (2)
UND TOT	34.0 ± 29.4 (6)[c]	70.1 ± 28.2 (30)	87.0 ± 9.9 (2)	80.0 ± 0.0 (2)
GRND TOT	90.5 ± 12.7 (6)[b]	69.9 ± 19.5 (30)	65.0 ± 24.0 (2)	84.0 ± 0.0 (2)
UND 14	22.2 ± 25.4 (6)[b]	80.7 ± 52.5 (30)	55.0 ± 9.9 (2)	38.5 ± 19.1 (2)
UND 58	4.5 ± 8.4 (6)	9.7 ± 8.4 (30)	19.0 ± 4.2 (2)	19.0 ± 7.1 (2)
UND GT9	0.7 ± 1.2 (6)[b]	4.3 ± 4.0 (30)	30.5 ± 6.4 (2)	14.0 ± 2.8 (2)
DBH LT25	1.5 ± 2.5 (6)	4.7 ± 5.7 (30)	3.0 ± 0.0 (2)	13.5 ± 12.0 (2)
DBH 2650	1.0 ± 0.9 (6)	2.7 ± 2.7 (30)	2.5 ± 0.7 (2)	2.0 ± 0.0 (2)
DBH GT50	0.8 ± 0.8 (6)	1.4 ± 1.3 (30)	2.0 ± 0.0 (2)	2.5 ± 2.1 (2)
BASAL	15.1 ± 11.1 (6)	30.7 ± 19.2 (30)	37.6 ± 0.6 (2)	32.0 ± 19.6 (2)

[a] $\bar{x} \pm$ SD (*N*).
[b] Dry lowlands and moist lowlands significantly different at $P < 0.05$ using a 2-tailed *t*-test.
[c] Dry lowlands and moist lowlands significantly different at $P < 0.01$ using a 2-tailed *t*-test.

vines and epiphytes at nest sites in our study areas paralleled the abundance of these plants in the environment (Richards 1952). Vines provide support for nests in trees that may otherwise lack adequate support, and they make the nest less conspicuous. The evergreen condition of the canopy and the abundance of vines and epiphytes make it difficult to find nests in humid tropical forests.

A lower percentage of nests was reused in consecutive years in Puerto Rico (6%) than in North America (17–50%) (Orians and Kuhlman 1956, Hagar 1957, Seidensticker and Reynolds 1971, Belyea 1976, Bohm 1978). This might be due to the abundance of nest sites in our study areas or to fast rates of nest decomposition. Dead branches and leaves in the canopy of tropical rain forests have been shown to decompose at rapid rates (Frangi and Lugo 1985); similar rapid decomposition of nest materials might reduce the rate of nest reuse.

Puerto Rican Red-tailed Hawks used a greater variety of tree species for nesting (ratio of tree species used to nests = 0.43) than do Red-tailed Hawks in North America (range of ratio = 0.03–0.38) (Bent 1937, Gates 1972, Belyea 1976, Mader 1978, Titus and Mosher 1981, Bednarz and Dinsmore, 1982), probably reflecting the higher diversity of tree species in Puerto Rico (Little et al. 1974). The most commonly used tree species (*Bucida buceras, Hymenaea courbaril, Casuarina equisetifolia, Cecropia peltata*) were also very common in their respective habitats (Birdsey and Weaver 1982). Due to their growth form, size, and location in the landscape, these tree species offered a wide view of the surrounding area.

Similarities among nest sites used by Red-tailed Hawks in widely different habitats and geographical areas suggest the use of similar nest-site selection criteria (Mosher et al., 1986). A survey of the literature reveals that Red-tailed Hawk nests in North America are associated with large trees, forest edges, open canopy structure, and steep slopes (e.g., Jackson 1891, Jessee 1901, Bent 1937, Orians and Kuhlman 1956, Mader 1978, Petersen 1979, Bednarz and Dinsmore 1982). Titus and Mosher (1981) found that most of these characteristics were significantly different from those expected if the nest site was selected randomly. These characteristics converge on two properties: they permit a bird at the nest to view a large portion of its breeding territory and permit the nest to be seen from a distance.

The pattern of nesting in open situations that offer a wide field of view from the nest has also been reported for other species of raptors (Newton 1979, Andrew and Mosher 1982, Gilmer and Stewart 1983, Green and Morrison 1983). Four explanations for this pattern have been proposed: (1) hawks need an open canopy to obtain unobstructed access to the nest (Orians and Kuhlman 1956, Mader 1978, Bednarz and Dinsmore 1982, Andrew and Mosher 1983), (2) they need wide views to detect predators at a distance (Belyea 1976, Blair and Schitosky 1982), (3) they need wide views to detect territorial intruders by using the nest as a surveying platform (Newton 1979), and (4) they use the visible nest as a territorial marker (Newton 1979). To this list we add a fifth explanation: adult Red-tailed Hawks spend a large portion of the day perched within their territory and they may need nests that are visible from these perches to detect aerial and scansorial predators approaching the nest. In rain and cloud forests adult Red-tailed Hawks seemed to prefer perches that offered a simultaneous view of their territory and their nest (Santana and Temple, in press).

Red-tailed Hawks probably choose nest sites that offer a wide view of their territory for many reasons, but territory defense could play an important role. Red-tailed Hawks are known to spend much of their flying time performing territorial displays and scanning their territories from perches (Ballam 1984, Janes 1984, Soltz 1984); territorial combat has been reported to last almost entire days (Janes 1984).

Red-tailed Hawks do not seem to select any one species of tree for nesting, and they also use cliffs and artificial structures (Smith and Murphy 1973, Olendorff et al. 1980). Red-tailed Hawks in Puerto Rico nested close to human activity; one pair nested successfully in an urban setting. This might be due to the high human densities on the island (400 people/km^2) (Birdsey and Weaver 1982). Nest sites that were very close to human activity were usually inaccessible to humans due to some factor other than horizontal distance (e.g., the presence of a river, fence, cliff, or other obstacle).

Red-tailed Hawks were not rare in Puerto Rico at the beginning of this century (Wetmore 1927, Danforth 1931), but their populations have apparently increased since the 1940s as agricultural lands and pastures reverted back to forest (Perez Rivera and Cotte Santana 1977, F. H. Wadsworth, pers. comm.). This land-use trend is no longer apparent, and during our study hunting, and nesting habitat were reduced in our lowland study areas as a result of development and urbanization. Unlike resident Broad-winged Hawks (*Buteo platypterus*) and Sharp-shinned Hawks (*Accipiter striatus*), which are uncommon in Puerto Rico due to their apparent need for large expanses of forest (Raffaele 1983), the wide habitat tolerances of Red-tailed Hawks have permitted them to remain common throughout the island. Increased habitat destruction, however, especially in lowland areas, will reduce nesting habitat for Red-tailed Hawks.

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